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## XIV.

*On the Affinities of the Genus VAVÆA, Benth. ; also of RHYTIDANDRA, Gray.*

By ASA GRAY, M. D.

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(Communicated to the Academy, October 10, 1854.)

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VAVÆA, a well-sounding name, formed from *Vavao*, one of the Friendly Islands, where the plant in question was discovered by the late Mr. Hinds, was employed Mr. Benthham to designate a genus, of obscure affinity, founded on a single incomplete specimen, destitute of fruit.\* No opinion as to its relationship was expressed, beyond the remark that it is evidently allied to *Ixionanthes* of Jack, — itself a genus most imperfectly known, and the family to which it belongs having scarcely even been guessed at. *Vavæa Amicorum*, Benth., the only species known, was likewise gathered by the naturalists of the Exploring Expedition in the Pacific under Captain Wilkes, both at the Friendly Islands (on Tongatabu) and at the Feejee Islands. In the first volume, recently published, of the Botany of this Expedition,† I endeavored to illustrate this genus, as far as could be done in the absence of ripe fruit and seeds (the former occurring on one specimen in a state barely far enough advanced to show that the ovary becomes a berry); and I ventured to append it to the order *Meliaceæ*, notwithstanding the stamens of more than double (usually triple) the petals in number, and the incomplete union of their filaments.

I have now had the opportunity of examining one or two blossoms from additional specimens, which clearly belong, I doubt not, to *Vavæa Amicorum*, although they differ

\* In Hooker's London Journal of Botany, 2. p. 212.

† Botany of the United States Exploring Expedition under Captain Wilkes; Phanerogamia, 1. p. 244, tab. 16.

from all those previously examined in having only twice as many stamens as petals, — conforming in this respect to the type of the andrœcium in the order *Meliaceæ*, except only that the filaments are not monadelphous to the top. The anthers being rather smaller than usual, and containing little good pollen, while the pistil is well developed, I am led to suspect that the difference may be attributable to sex, and that the flowers may be more or less polygamous, as in *Aglaia*, &c.; which is the more probable, inasmuch as these occur on a specimen which bears, on a lower and earlier inflorescence, some nearly mature fruit. It was apparently these decandrous blossoms that misled Mr. Rich, the Botanist on the Expedition, preventing him from recognizing the plant which he had previously marked as a probable relative of *Canella*,\* while these specimens were ticketed and even figured as a *Styrax*. The drawing of the plant was accompanied by some erroneous analyses, in which I had failed to identify the *Vavæa*, and therefore had left the specimens among other *Styracaceæ* without examination until now.

The fruit of *Vavæa* proves to be a berry, as was anticipated from the fertilized and half-grown ovary. It is rather dry, four or five lines in diameter, subtended by the small persistent calyx, and three-celled or four-celled by thin dissepiments, which perhaps are obliterated when only one seed matures. A single seed is sometimes matured in each cell; and in one instance both ovules were fertilized in the same cell. The seeds are oval, about three lines long, smooth, destitute of any arillus, ascending from near the base of the cell, closely sessile; the linear hilum being attached directly to the axis of the fruit without any funiculus: the testa chartaceous, or perhaps somewhat fleshy, its whole base occupied by a large orbicular chalaza, which is connected with the hilum by an extremely short rhaphe. The hilum extends from near the base to about the middle of the seed. There is a rather fleshy inner integument of the seed, but no albumen. The embryo consists of a pair of orbicular-oval, plane, flat or plano-convex, fleshy, peltate cotyledons, which are cordate by a narrow and deep sinus: the radicle is superior, remote from the hilum, slender, but wholly retracted and concealed within the sinus.

The carpological characters, therefore, manifestly confirm the suggested relationship of this genus to the *Meliaceæ*, where the exalbuminous embryo assigns it to the tribe *Trichilieæ*.

Simple and undivided leaves occur, as is well known, in three genuine Meliaceous genera. The cup-shaped disc is partially united with the andrœcium in *Trichilia*, *Eke-*

\* Botany of United States Exploring Expedition, l. c. p. 246.

*bergia*, &c.; and in *Mallea*\* it is as completely adnate as in *Vavæa*, while the andrœcium is as deeply divided. The only remaining peculiarity, that of the increased number of stamens, is now found not to be a constant one, nor is it wholly irreducible to the type of the Meliaceous andrœcium, whatever particular hypothesis may be adopted in respect to the nature of its interposed lobes or naked teeth.

Although no doubt remains that *Vavæa* is a truly Meliaceous genus,† it is by no means surprising that Mr. Rich, without investigating the ovules and seeds, should have even referred these diplostemonous specimens to *Styrax*. The floral envelopes equally vary from four to seven in both, even in the same species; the general conformation of the pistil is similar; the uniserial stamens, monadelphous below, and even the beard on the inner face of the filaments, are equally points of resemblance; while the freedom of the andrœcium from the corolla, both organs being hypogynous, has its counterpart in *Styrax Benzoin* and some other species.‡

\* *Adr.* Jussieu, *Mem. Meliac.* t. 15, f. 6, and t. 17, 18, &c.

† The completed character of the genus is subjoined:—

VAVÆA, *Benth.*

Calyx 4–7-fidus, persistens; lobis triangulari-ovatis æstivatione leviter imbricatis. Petala lobis calycis numero æqualia, hypogyna, ligulato-oblonga, utrinque sericeo-puberula, æstivatione convoluta-imbricata, decidua. Stamina numero petalorum dupla vel sæpius tripla aut subtripla, ab iis libera: filamenta plana, linearia, basi glabra in tubum disco hypogyno cupuliformi tenui adnatum monadelpha, superne libera, intus barbato-villosissima, apice acuto antheram bilocularem (loculis longitudinaliter dehiscentibus) introrsam fere basifixam gerentia. Pollen globosum. Ovarium ovoideum, basi lata sessile, 3–4-loculare: stylus columnaris: stigma peltatum, 3–4-radiatum. Ovula in loculis gemina, angulo centrali prope basim inserta, collateralia, adscendentia, subamphitropa; micropyle supera. Bacca globosa, 3–4-locularis. Semina in loculis abortu solitaria rariusve bina, ovalia, adscendentia, exarillata; testa lævi chartacea; hilo lineari chalazæ magnæ basilari proximo; rhaphe brevissima. Albumen nullum. Cotyledones carnosæ, plano-convexæ, suborbiculares, sinu profundo cordatæ, radiculam gracilem superam prorsus includentes. — Arbuscula glabella; foliis simplicibus integerrimis alternis obovato-oblongis obsolete punctatis; stipulis nullis; pedunculis axillaribus multifloris; floribus cymosis parvulis (forte polygamis).

*Vavæa*, *Benth.* in *Lond. Jour. Bot.* 2. p. 212; *Gray*, *Bot. Phanerog. U. S. Expl. Exped.* 1. p. 244, t. 16.

‡ Endlicher (*Gen.* p. 743), following Jussieu, assigns to *Styrax* a free calyx and a perigynous corolla;—two characters which I have not found to coexist in this genus. Alph. De Candolle, following Richard (in Michaux, *Fl.* 2. p. 41), describes the base of the calyx-tube as adherent to the base of the ovary, which is the case in the North American species, and most others. Zuccarini (*Fl. Japon.* 1. p. 54, t. 23), indeed, describes and figures *S. Japonicum*, a species of the same group as the North American ones, with both the

In this light we may admire the sagacity of Jussieu,\* and of De Candolle,† who so long ago indicated a probable affinity between *Styrax* and the *Meliaceæ*; while the younger De Candolle expresses a reasonable doubt whether his own tribe *Pamphilieæ*, annexed to *Styracaceæ*, may not rather belong to the former order.‡ The seed and embryo of *Styrax* very well accord with those of most *Meliæ*; so do those of *Foveolaria* as far as known; those of *Pamphilia* have not been investigated. The valvular, the convolute-imbricative, and the quincuncial æstivation of the corolla, no less than the union or the want of union between the base of the corolla and of the andræcium, which occur in different Meliaceous genera, are severally represented in different species of *Styrax*.§ The stellular pubescence or scurf of *Styrax* is of no particular

calyx and the corolla hypogynous: but the specimens communicated from the Leyden herbarium plainly exhibit the calyx adnate to the base of the ovary, the corolla, as in other cases, inserted at the line of junction. In *S. Benzoin*, however, both the calyx and the corolla are completely free and hypogynous; but this character does not hold in the few South American species I possess, which have a similar valvate corolla, namely, *S. Camporum*, *S. Gardnerianum*, *S. tomentosum*, and *S. ovatum*; although it must in some others, since a species under the name of *S. leiophylla* is so figured in Lindley's Vegetable Kingdom, ed. 3, p. 593 b, from a sketch by Mr. Miers, who, in the accompanying letter-press, inadvertently assigns an "ovary superior, wholly free from the calyx," as a character of the order *Styracææ*.

\* "An genus potius polypetalum indeque Meliis affine?" — Gen. Pl. p. 156.

† "An *Styrax*, Quivisiæ et Turræa habitu similis, huc revocanda." — Prodr. 1. p. 619.

‡ Prodr. 8. p. 270. — Mr. Bentham, also, in Trans. Linn. Soc. 18. p. 231, indicates the alliance of *Styracææ* as an order, in the first instance with *Ebenaceæ* and *Humiriaceæ*, and in the next place with *Meliaceæ*.

§ M. Alph. De Candolle describes the æstivation of the corolla of *Styrax*, from *S. officinale*, as "parum constante, initio sinistrorsum convoluta, demum subvalvari." I find it in that species, and all the North American ones except *S. Americanum*, with the petals pretty strongly overlapping in the bud; very rarely, however, in an unbroken convolute series, but for the most part convolute-imbricate, — one petal being wholly exterior while the adjacent one is wholly interior, — just as the æstivation of *S. Japonicum* is correctly figured by Zuccarini (in Fl. Japon. 1. t. 23, f. 1): and in some instances this varies to nearly the regular quincuncial imbrication. But in *Styrax Americanum* the æstivation is valvular, with one or two of the conjoined margins more or less introflexed, often unequally so; while in *S. Benzoin*, as also in all of the few South American species I have examined, it is more strictly valvular. Mr. Miers must have contemplated these species only (overlooking *Pterostyrax* and *Halesia* likewise) in attributing a valvate æstivation to the corolla of the whole order *Styracææ*, as he limits the group (in Lindley's Vegetable Kingdom, l. c.). Moreover, although the andræcium is sometimes unconnected with the corolla, as in *Styrax Benzoin*, already mentioned, yet it is far from being "generally free from the petals" throughout the genus.

A few other discrepancies in the characters of *Styrax*, of more or less importance, may be noticed in passing. Endlicher (I cannot at this moment ascertain whether the observation originated with him) gives the character, "ovula . . . . inferiora horizontalia vel adscendentia, superiora sæpius pendula"; and this

consequence in a question of affinity, since it occurs in so many plants of widely different families ; but it equally exists in many *Meliaceæ*.

Nevertheless, the stronger tendency of *Styrax* and of the *Humiriaceæ* would appear to be in another direction, although the limits between the *Styraceæ* and the *Meliaceæ* cannot be determinately fixed, until the seeds of *Pamphilia* and *Foveolaria* are properly known. But it is singular that so acute a botanist as Mr. Miers, who proposes to separate *Styrax* widely from the *Symplocineæ*,\* — allowing only a distant relationship

phrase, with a slight and unimportant transposition, is repeated by Alph. De Candolle in his character of the genus. On the other hand, Mr. Miers, in his character of the family and his analysis of a *Styrax*, already referred to, states of the ovules, that they have the “upper row erect, the middle horizontal, the lower pendulous.” In no species have I been able to verify the former statement ; that of Mr. Miers is borne out by *S. officinale*, *S. grandifolium*, and some other species. But this is not true of the whole genus. Zuccarini describes the ovules of *S. Japonicum* as *all erect* ; the plate represents them as all ascending (which is doubtless what was meant), as inspection shows them to be ; and so I believe they are in *S. Americanum* and some other American species.

Mr. Miers also describes and figures the ovary of *Styrax* as “trilocular only at the base, but unilocular at the summit,” and naturally refers to this character as confirming the relationship of *Styraceæ* with the *Olaceæ*. I do not find it so in the species I possess, but rather with the dissepiments extending quite to the summit of the ovary, although early separating from the ovuliferous axis as the ovary enlarges ; that is, “parietibus incompletis ab axi centrali demum distantibus,” as stated by M. Alph. De Candolle.

A more anomalous character, attributed, by Mr. Miers alone, to the ovary (not only of *Styrax*, but of the order *Styraceæ* as he limits it), namely that of bearing “a remarkable depressed epigynous gland upon its apex,” I am wholly unable to confirm. In *Styrax tomentosum*, and to some extent in *S. camporum*, the ovary may be observed of nearly the shape delineated in Mr. Miers’s sketch (l. c. fig. 4), that is, constricted below ; but what answers to the “epigynous gland” is only the ordinary epidermis of the ovary with its downy covering, unaffected by the pressure of the base of the corolla and the staminal tube which closely encircles the lower part, and it readily separates from the rest of the parietes, as it also does in *S. Benzoin*.

\* Without pronouncing here upon the propriety of such separation, it may be remarked that the *Styraceæ* certainly appear to be closely connected with the *Symplocineæ* through *Pterostyrax* and *Halesia* ; and that a diagnosis between the two groups, as limited by Mr. Miers, is not successfully based upon any one of his differential characters, enumerated in Lindley’s Vegetable Kingdom, p. 593, b. For, 1. A “tubular and entirely free calyx” belongs merely to a part of the genus *Styrax*, and not at all to *Pterostyrax* and *Halesia*. 2. The same remark is true of “the valvate æstivation of the petals.” 3. “Their stamens being always uniserial” does not exclude *Barberina*, in one species of which, moreover, they are only thrice the number of the petals : in *Halesia tetraptera* the stamens are sometimes four times the number of the lobes of the corolla. 4. “Linear anthers dorsally affixed to broad filaments nearly of their length,” are not attributable to *Pterostyrax* and *Halesia*, nor to some species of *Styrax*. 5. The same objection applies to a “superior ovary with three incomplete dissepiments” and “a free central placentation,” which besides are not true of *Pamphilia* ; and the ovules are as numerous in certain *Symplocos* as in some *Styraces*.

between them through the *Ebenaceæ*, — should at the same time ignore any affinity between the *Meliaceæ* and his *Styraceæ*, especially while the latter family is made to include *Pamphilia* and *Foveolaria*.

RHYTIDANDRA \* is a genus established on a specimen of a shrub or arborescent plant, with unexpanded flowers only, in the collection of the United States Exploring Expedition, from one of the Feejee Islands. It was referred to the *Olacaceæ*; but with some misgiving, on account of the complete and immediate adhesion of the calyx to the surface of the ovary; which, moreover, is strictly one-celled, and with a single ovule suspended from the very apex of the cell, without the intervention of any placental column or any trace of sterile cells. I had remarked, that, “if rightly referred to this order, it must be viewed as a genus whose affinity tends towards *Styracaceæ* rather than *Santalaceæ*.”† This floral structure should have led me at once to consider the relations of the plant to *Alangium* and *Marlea*; but, possessing no materials of, and no previous acquaintance with, the *Alangieæ*, I overlooked what I now perceive to be the nearest affinity of *Rhytidandra*.

The leaves of this plant, with their transverse veinlets and oblique base; the axillary cymose inflorescence; the adnate and scarcely toothed calyx; the long and narrow petals, borne, like the stamens, on the margin of an epigynous disc; the linear and introrsely adnate anthers; the bearded filaments, such as they are (for they are extremely short); the solitary and suspended anatropous ovule; and the elongated style, are all points of perfect agreement with the *Alangieæ*.

6. “A solitary one-celled putamen having a single erect seed” would commonly exclude *Pterostyrax* and *Halesia*, and does not well apply to *Styrax*; the albumen is equally “copious and fleshy” in *Symplocos*; and the embryo of *Halesia* appears to be quite intermediate between that of the *Symplocineæ* and that of *Styrax*, some species of which exhibit little or no stellate pubescence. The petals in both species of *Halesia*, although in some blossoms perhaps merely “agglutinated at the base by the membranaceous ring of the stamens,” in others are truly “confluent into a gamophyllous tube” far above the attachment of the andræcium, the ring of which, moreover, is sometimes but imperfectly adnate to the base of a gamopetalous corolla.

The *Humiriaceæ* are well marked by one or two decisive technical characters; but nothing appears to forbid their annexation to the *Styracaceæ* while that family includes the *Symplocineæ*.

\* Botany of the United States Exploring Expedition under Captain Wilkes: Phanerogamia, p. 302, t. 28.

† It should be stated that Mr. Miers, who has, perhaps, a more profound and extensive acquaintance with the *Olacaceæ* and their immediate allies than any other botanist, and who has most ably illustrated them, on reading the published characters of *Rhytidandra*, immediately expressed to me, in a letter, his opinion that the genus belonged neither to his  *Icacineæ* nor *Olacineæ*. He suggested, instead, an affinity with the *Loranthaceæ*.

The only observed discrepancies are the valvular æstivation of the corolla in *Rhytidandra*, and its bifid style; — neither of which characters is likely in the present case to indicate more than a generic distinction. For the flattened divisions of the style, themselves more or less bifid at their summit, would by a further union produce nearly such a four-lobed stigma as that of *Marlea* and of *Alangium*. And if the narrow petals are really convolute in æstivation in the former as well as the latter genus, their margins can but slightly overlap,\* while the strictly valvate mode would be no unexpected character in a new genus of a small group, which — following Mr. Brown's suggestion made thirty-six years ago — it is now conceded must be merged in the *Cornaceæ*.†

In its unilocular ovary, *Rhytidandra* accords with *Alangium*, as also with an occasional state of *Marlea*; ‡ while the stamens correspond with those of *Marlea* in number and position, and have even shorter filaments. The anthers are distinct, not connate into a tube, as those of *Marlea* are said to be by Lindley and by Endlicher (but not by De Candolle); nor are the stamens united by pairs, as those of *Marlea* are characterized and represented by Lindley; unless, indeed, what I had taken for a quadrilocellate anther should consist, as it possibly may, of a pair of closely coalescent anthers. Their dehiscence, if known, would determine this point. In respect to it I can only say that, if the anthers of *Rhytidandra* really open longitudinally at all, they must do so by the lateral grooves, one on each side, which correspond with an internal partition, longitudinally dividing each half of the organ into two locelli; and in that case the whole must constitute a single stamen, as I had supposed it to do; and I suspect this is the case in *Marlea* also.

However this prove to be, *Rhytidandra* is sufficiently distinguished from *Marlea* by its moniliform and chambered anther-cells, its one-celled ovary, and its bifid style with elongated and slender but flattened lobes.

This peculiarity of the style is of considerable interest; for the lobes may be justly compared with the style of *Nyssa*; the affinity of which to the *Alangieæ* was happily suggested (though with doubt) by Brongniart,§ while its relationship to the *Corneæ* was practically recognized by Blume, who referred his genus *Mastixia* first (and justly)

\* Wight and Arnott's authority (Prodr. Fl. Ind. Or. 1. p. 325) should settle the point, at least for *Alangium*. But the figure of *Marlea begoniæfolia* in Bot. Reg. 24, t. 61, appears as if the petals were valvate.

† Bennett, Plantæ Javanicæ Rariores, p. 194. In collating *Marlea* with the *Corneæ*, no difference in æstivation is here mentioned; from which it may be inferred that the petals of the former genus are valvate.

‡ Lindley, Bot. Reg. l. c. Clarke, in Kew Jour. Bot. 2. p. 129.

§ Enum. Pl. Hort. Mus. Par. p. xxx. note.



to the *Corneæ*, and then to *Nyssaceæ*.\* Lindley has adopted Brongniart's suggestion, and referred both *Nyssa* and *Mastixia* to the *Alangiaceæ*.†

I may add, that the fertile flowers of *Nyssa* sometimes exhibit a double perianth, namely, five minute rounded lobes or teeth belonging to the border of the adherent calyx, and alternate and within these as many small, ovate petals.

\* \* \* (November 13.) Flower-buds of *Marlea begoniæfolia*, received through the kindness of Sir William Hooker just as this sheet is about to go to press, verify the suggestions given on the preceding page, both in respect to the æstivation of the corolla, which is truly *valvate*, and as to the nature of the anthers, which are *simple and quadrilocellate*, not united in pairs as described by Lindley. Nor, in the flower-buds examined, are the anthers in the least coalescent into a tube. The generic character assigned by De Candolle is therefore correct as far as it goes. That of Endlicher is incongruous as regards the stamens, he having adopted the view of Lindley without consistently carrying it out, and erroneous as to the æstivation of the corolla, probably from having transferred this point of Wight and Arnott's character of the *Alangieæ* to the genus *Marlea*. The relationship between *Rhytidandra* and *Marlea* is therefore immediate. The essential differences between them are correctly enumerated in a preceding paragraph.

\* Museum Bot. Lugd.-Bat. p. 256.

† Vegetable Kingdom, pp. 719, 720.